THE EFFECTS OF ALTERNATING LONG AND SHORT DAILY PHOTOPERIODS ON GONADAL GROWTH AND PITUITARY GONADOTROPINS IN THE WHITE-CROWNED SPARROW, ZONOTRICHIA LEUCOPHRYS GAMBELII [1]

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The photoperiodic induction of the development of gonads in many species of birds of mid and high latitudes has become an extensively investigated phenomenon. (See Farner, 1959, 1961; Farner and Follett, 1966; Wolfson, 1966, for reviews.) An interesting characteristic of the response, at least in some species, is that the stimulatory photoperiod need not consist of an uninterrupted daily period of light; it may instead be replaced effectively by a series of flashes of light following an otherwise nonstimulatory photoperiod, or simply by a daily series of adequately spaced short photoperiods. (See, for example, Benoit, 1936; Burger, Bissonnette, and Doolittle, 1942; Straffe, 1950; Jenner and Engels, 1952; Farner, Mewaldt, and Irving, 1953; Farner, 1958, 1959, 1964b, 1965a; Wolfson, 1959a,b,c,d, 1960, 1966.) Earlier investigations of this characteristic of the photoperiodic testicular response in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) led to the hypothesis of a "carry-over period" (Farner, Mewaldt and Irving, 1953; Farner, 1958, 1959, 1964a) that rationalized the induction of growth of the testes in response to flashes of lights by assuming the persistence of a light effect into the ensuing dark period. More recently the interpretation of responses to interrupted light has been complicated by the discovery (Hamner, 1963, 1964, 1965) of a circadian function in the mechanism of photoperiodic testicular response of the House Finch (*Carpodacus mexicanus*). Similar functional relationships have been confirmed for the House Sparrow (*Passer domesticus*) by Menaker (1965), for the Slate-colored Junco (*Junco hyemalis*) and the Bobolink (*Dolichonyx oryzivorus*) by Wolfson (1965a, b, 1966), and for *Z. l. gambelii* by Farner (1964b, 1965b). Farner (1965b) presented evidence that suggests that the nature of this circadian component in *Z. l. gambelii* is a periodicity in photosensitivity of the response mechanism.

These demonstrations of a circadian function in the response mechanism have necessitated modification of the original "carry-over" hypothesis. This modification is based on a summation of derived rates from the photosensitivity curve (Farner, 1965b) for a series of daily photoperiods of increasing duration (8L 16D through 20L 4D to continuous light) and a comparison of the rates obtained by summation with those based on direct measurements of responses to the same series of photo-

[1] The investigation described herein was supported by a grant (GB-1380) from the National Science Foundation.

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periodic treatments (Farner and Wilson, 1957). The rates obtained by summation were found to exceed the measured rates as a regular function of the duration of the photoperiod. The simplest explanation for this relationship is that the rates presented by Farner (1965b) must include "carry-over effects" from the 2-hour photoperiods and that the magnitude of the "carry-over effect" also is a function of the cycle in photosensitivity.

Although direct evidence is lacking, it appears that the "carry-over" effects from brief flashes (1–10 seconds) are of short duration and are probably associated with the function of receptors or neural transmission (Farner, 1958). Other functions that could provide possible bases for "carry-over effects," especially of longer duration, include the release and transport of neurohormone from the median eminence, release of gonadotropin from the adenohypophysis, the survival time of gonadotropin in the circulating blood, and the nature of the action of gonadotropin on the growth processes of the gonad. There is now experimental evidence for the existence of "carry-over effects" of long duration (hours or days), that may be explainable on the basis of one of these mechanisms. For example, in *Carpodacus mexicanus* a stimulatory photoperiod has a growth-promoting effect on the testes for as long as 72 hours after the cessation of the photoperiod (Hamner, 1964). The experiments described herein were designed to investigate further these long-persisting "carry-over effects" in *Zonotrichia leucophrys gambelii* by subjecting birds to a variety of cyclic photoperiodic treatments. It is the function of this paper to communicate the results of these experiments with respect to the rate of development of the gonads and the concentration of gonadotropin in the adenohypophysis.

The Experiments

Basic to the design of the experiments are certain characteristics of photoperiodically induced gonadal growth in *Zonotrichia leucophrys gambelii* (Farner and Wilson, 1957; Farner, 1959, 1964b; Farner *et al.*, 1966). Of primary importance is the logarithmic nature of testicular growth from resting weight (*ca.* 2 mg.) to *ca.* 250 mg. and of ovarian growth from resting weight (*ca.* 5 mg.) to *ca.* 50 mg. under photoperiodic stimulation. The relationship between gonadal weight and time subjected to fixed daily stimulatory photoperiods may be expressed quite accurately by:

$$\log W_t = \log W_0 + kt$$

where W_0 is the resting gonadal weight (in mg.), W_t is the gonadal weight on day t after the beginning of photoperiodic stimulation, t is time (in days), and k is the logarithmic growth-rate constant (in days $^{-1}$).

For these experiments we adopted initially the admittedly oversimplified working hypothesis that each long day causes a fixed logarithmic increment of gonadal growth even though isolated by intervening days with short, non-stimulatory photoperiods. It was assumed that the short, non-stimulatory photoperiods make no positive contribution to gonadal growth, a reasonable assumption since males show no demonstrable growth after many months on 8-hour daily photoperiods (Farner and Wilson, 1957). Although there is a small non-photoperiodic growth of the ovary under such conditions (Farner *et al.*, 1966), it is negligible within the context of these experiments. Thus groups of birds were subjected to a variety

of cycles of the type L nS (L = day with long, stimulatory photoperiod; S = day with short, non-stimulatory photoperiod; n refers to the number of short days interposed between long, stimulatory days; it may take the value of 0 or any integer).

If the working hypothesis were correct, it follows that k expressed in cycles $^{-1}$ (rather than days $^{-1}$), should be constant for all groups. A value of k (in cycles $^{-1}$) greater than that obtained with daily stimulatory photoperiods ($n = 0$) would then be quantitative evidence for a "carry-over effect." Conversely a value of k less than that obtained with daily stimulatory photoperiods would be evidence for significant gonadal regression between the days with long daily photoperiods.

From previous experience with *Zonotrichia leucophrys gambelii* we selected a 20-hour photoperiod (followed by four hours of dark) for the long day (L) and an 8-hour photoperiod (followed by sixteen hours of dark) for the short day (S).

Experiment I. Birds were captured from migrant flocks during early and mid-September. On 30 October they were transferred indoors and held on 8-hour daily photoperiods (09:00–17:00) until exposure to the experimental lighting regimens. Six groups of 15–20 birds each were submitted to the following treatments: *Group* L_1, a long daily photoperiod every day beginning on 16 November; *Group* L_2, the same regimen but beginning on 24 December; *Group L S,* alternating days with long and short daily photoperiods; *Group L 2S,* repeated cycles of one day with long daily photoperiod followed by two days with short daily photoperiods; *Group L 3S,* repeated cycles of one day with long daily photoperiod followed by three days with short daily photoperiods; *Group L 5S,* repeated cycles of one long day followed by five days with short daily photoperiods. Control Group L_2 was necessary because of the increase in photosensitivity that occurs as a function of time held on short daily photoperiods (Laws, 1961; Farner, 1962; Farner and Follett, 1966). The number of cycles, varying from 20 for L_1 and L_2 to 10 for Group L 3S, was determined by the rate of testicular growth. All birds were killed when the combined testicular weight was about 100 mg. or when the ovarian weight was about 30 mg. and therefore within the linear portion of the logarithmic growth curve (Farner and Wilson, 1957; Farner *et al.,* 1966). The control birds were killed at 10:00, one hour after the beginning of the photoperiod. All other birds were killed at 10:00 on the first short day in their respective cycles.

Experiment II. In principle, this experiment was similar to Experiment I except that more highly photosensitive birds were used. First-year males were captured during autumn migration or from the over-wintering population in the Snake River Canyon near Pullman. They were moved from outdoor aviaries to indoor cages and 8-hour daily photoperiods on 29–31 January. Subsequently they were divided into four groups (12–14 per group) as follows: Group L, Group L 2S, Group L 3S and Group L 5S. The photoperiodic schedules were identical with those for the corresponding groups in Experiment I. The experimental photoperiodic regimens were begun on 11 March.

Experiment III. This experiment was an attempt to identify the periods of synthesis and release of gonadotropin in birds subjected to a photoperiodic cycle with both long and short daily photoperiods. The particular regimen selected was L 3S; the experiment was begun with 39 first-year birds on 11 March. After ten complete cycles birds were killed on the following schedule: At the beginning and

TABLE I

The effect of alternation of long days and short days on the rate of testicular growth in Zonotrichia leucophrys gambelii

Group	Experiment I		Experiment II	
Photoperiodic cycle*	Rate of testicular growth (k)** $days^{-1}$	Rate of testicular growth (k)*** $cycles^{-1}$	Rate of testicular growth (k)** $days^{-1}$	Rate of testicular growth (k)*** $cycles^{-1}$
L_1	0.099 ± 0.012	0.099	0.111 ± 0.011	0.111
L_2	0.106 ± 0.010	0.106	——	——
L–S	0.087 ± 0.009	0.173	——	——
L-2S	0.072 ± 0.007	0.216	——	——
L-3S	0.064 ± 0.008	0.256	0.065 ± 0.005	0.260
			0.064 ± 0.006****	0.256****
L-5S	0.031 ± 0.018	0.183	0.034 ± 0.013	0.204

* L = "long day" (20 hours light, 4 hours dark); S = "short day" (8 hours light, 16 hours dark).

**k = (log W_t − log W_o)/t where W_o is gonadal weight at day O, W_t is gonadal weight at day t, and t is time in days. Mean and 95% confidence limits.

*** k with t measured as number of photoperiodic cycles.

**** From Experiment III.

the end of the long daily photoperiod in the 11th cycle, and at the ends of the short photoperiod and the long dark period of the first short day thereafter, and at the beginning and the end of the short photoperiod and at the end of the long dark period on the final short day of the cycle (Fig. 3).

Experiment IV. This experiment was designed to determine the time required after the discontinuation of a stimulatory photoperiod for gonadal regression to become apparent. A group of 38 males, drawn from the same population as in Experiment II, was subjected to 20-hour daily photoperiods and was then changed to 8-hour daily photoperiods. Samples of eight were taken before (09:00) and after (05:00) the last long photoperiod and at the beginning of the short daily photoperiod (09:00) on the 3rd, 7th, and 11th days after discontinuation of long daily photoperiods.

MATERIALS AND METHODS

The experimental birds were captured with Japanese mist nets and held under natural conditions of photoperiod and temperature in large outdoor aviaries until they were moved into small indoor cages in constant condition rooms. Only first-year birds were used. Drinking water and a nutritionally adequate chick-starter mash were freely available. Illumination indoors was provided by incandescent lamps; intensity at the cage floor was at least 400 lux. The temperature was maintained at 21 ± 1° C.

In all experiments the birds were killed by decapitation. Gonads were removed and preserved in a mixture of 10% formaldehyde, 10% acetic acid, 30% ethanol, and 50% water v/v. After five days they were transferred to 70% ethanol; five days later they were weighed on a precision torsion balance. Pituitaries were removed immediately after killing and placed in dry acetone which was changed

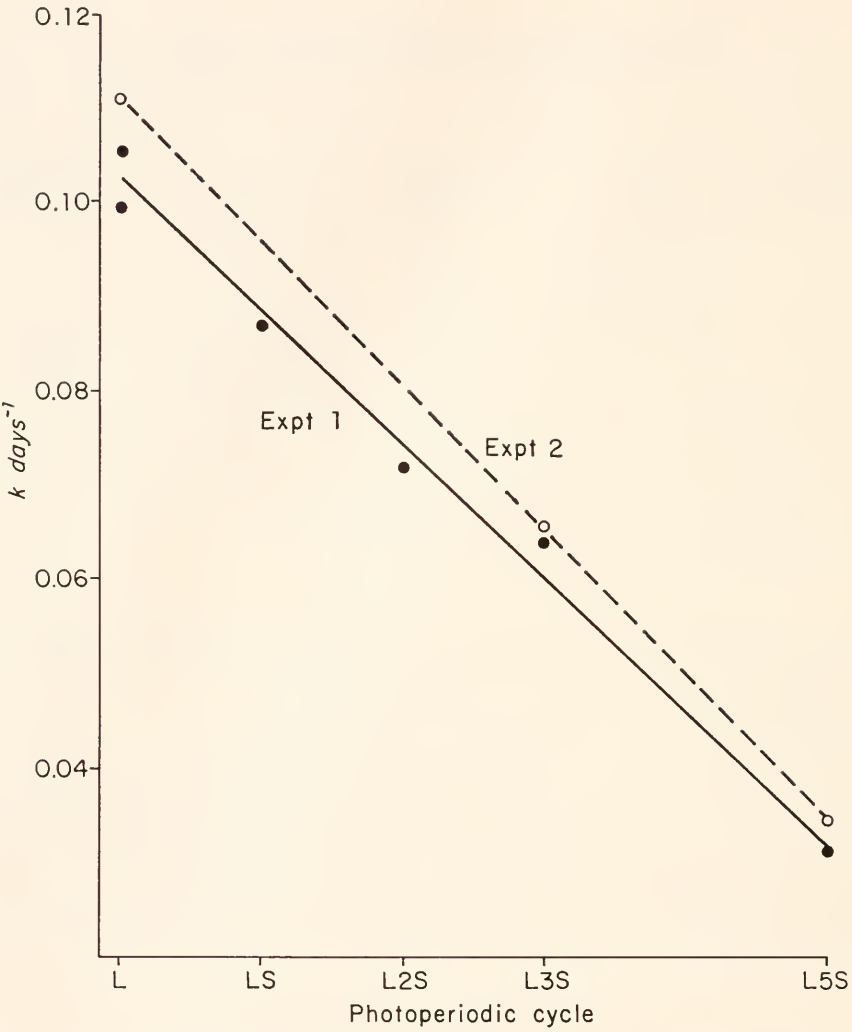

FIGURE 1. Testicular growth rates of *Zonotrichia leucophrys gambelii* as a function of short days (8L 16D) interposed with long days (20L 4D). The birds used in Experiment II had been held longer on short days and were therefore more photosensitive. —— Experiment I. – – – Experiment II.

twice over the next four days. The glands were then air-dried and stored *in vacuo* at 0° C. over phosphorus pentoxide until assay.

Gonadotropins were assayed by the method of Breneman *et al.*, (1962) as modified by Follett and Farner (1966). Glands from several birds were normally pooled and a single assay of the 2 + 2 type performed with 8–10 chicks at each dose level. The results from each assay were subjected to a full analysis of variance (Bliss, 1952). Potency estimates are given, together with 95% confidence

TABLE II

The effect of alternation of long days and short days on the rate of ovarian growth in Zonotrichia leucophrys gambelii Experiment I

Group / Photoperiodi cycle*	Rate of ovarian growth (k)** days^{-1}	Rate of ovarian growth (k)*** days^{-1}
L_1	0.034 ± 0.010	0.034
L_2	0.043 ± 0.009	0.043
L-S	0.029 ± 0.005	0.057
L-2S	0.028 ± 0.006	0.084
L-3S	0.022 ± 0.005	0.087
L-5S	0.013 ± 0.003	0.052

* See Table I.

** $k = (\log W_t - \log W_0)/t$ where W_0 is gonadal weight at day 0, W_t is gonadal weight at day t and t is time in days. Mean and 95% confidence limits.

*** k with t measured as number of photoperiodic cycles.

limits and the index of precision (λ). The latter is the ratio of the standard deviation to the slope of the dose-response curve. The values of λ compare favorably with other gonadotropin assays. When gonadotropins were estimated throughout the L3S cycle in Experiment III individual glands were assayed (2 + 1 assay). The potency values for each determination were used and subjected to standard statistical procedures for calculations of means and standard errors; comparisons of means were made by Fisher's t test.

RESULTS AND DISCUSSION

The testicular growth rates in Experiments I and II are shown in Table I. The difference in rates between groups L_1 and L_2 in Experiment I and between L_1 of Experiment I and L_2 of Experiment II, although in themselves not statistically significant, are nevertheless consistent with previous observations of increasing photosensitivity as a function of time of exposure to short daily photoperiods (Laws, 1961; Follett and Farner, 1966). As expected, the testicular growth rates, expressed as days $^{-1}$, decreased as a function of the number of short days per cycle (Fig. 1; for Experiment I, $r = 0.98$, $P < 0.01$). However, the slope of the line is small so that the testicular growth-rate constant (in cycles $^{-1}$) is a positive function of the number of short days per cycle up to a maximum for Group L 3S (Table I). The growth-rate constant (in cycles $^{-1}$) for Group L 5S was smaller than that for Group L3S but nevertheless greater than those of the L groups. The ovarian growth-rate constants showed the same pattern although characteristically lower (Table II). The responses of the females were consistent with the hypothesis (Farner *et al.*, 1966) that up to an ovarian weight of about 50 mg. the photoperiodic control mechanism is similar to that of males.

Experiment IV, which was designed to test for testicular regression, showed that the mean weight of the testes increased from 95.6 mg. at the end of the long daily photoperiods to 131.7 mg. after three short days and 146.7 after seven short days. Regression was detected only by eleven short days when the mean testicular

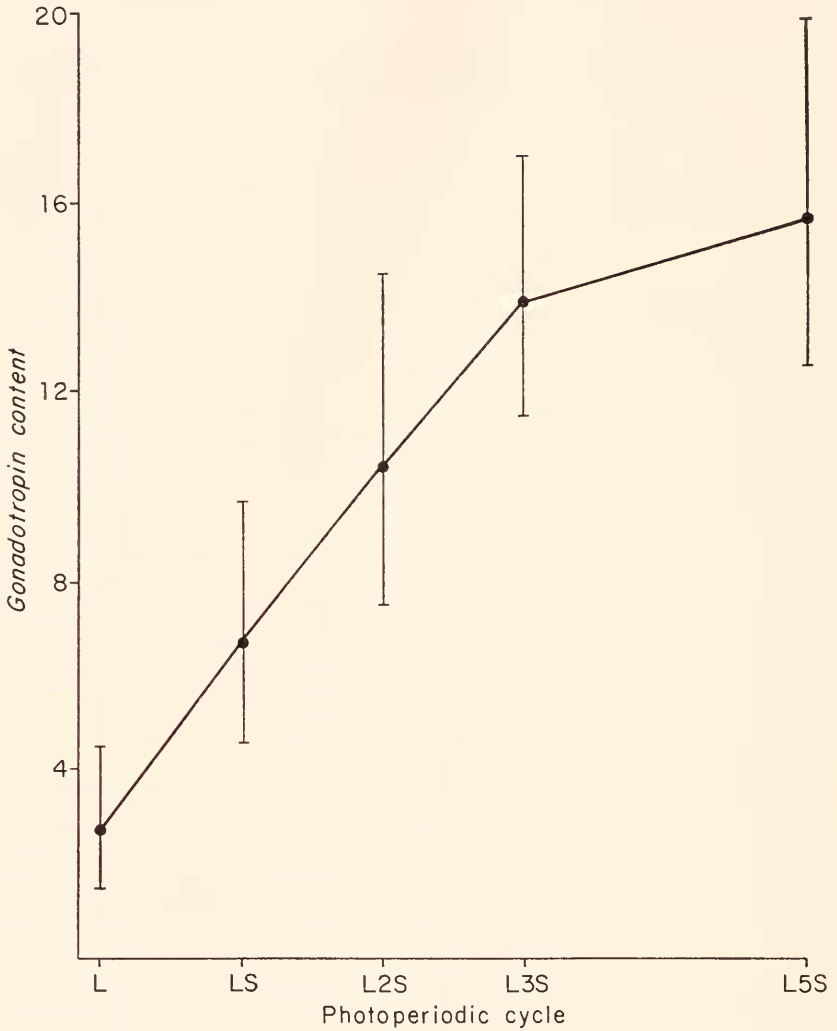

FIGURE 2. Gonadotropin content of the anterior pituitary gland of males (*Zonotrichia leucophrys gambelii*) in μg. equivalents of NIH-LH as a function of short days (8L 16D) interposed with long days (20L 4D). Vertical bars define the 95% confidence limits.

weight was 76.7 mg., a value significantly lower ($P < 0.05$) than the weight after seven short days.

A recent series of ingenious experiments by Wolfson (1966) inject a further parameter into the performance of photoperiodic mechanisms. With *Junco hyemalis* it was found that the photoperiodically induced gonadal growth initiated with 16L 8D continued for as long as 18 days in uninterrupted continuous darkness, during which time the birds showed a long-day circadian periodicity in motor activity. Birds that were changed to a short-day regime (9L 16D) instead of

TABLE III

The effect of alternation of long days and short days on the concentration of gonadotropin in the anterior pituitary gland of male Zonotrichia leucophrys gambelii

Group	Experiment I		Experiment II	
Photoperiodic cycle*	Gonadotropin Content per gland** μg. equivalents	λ***	Gonadotropin Content per gland** μg. equivalents	λ***
L_1	2.7 (1.6– 5.0)	0.195	16.7 (11.5–21.9)	0.159
L_2	6.2 (4.6– 9.6)	0.152	——	——
L-S	6.7 (4.6– 9.8)	0.107	——	——
L-2S	10.4 (7.1–15.2)	0.108	——	——
L-3S	13.9 (11.5–16.9)	0.117	21.8 (15.4–29.6)	0.174
L-5S	15.7 (12.4–20.1)	0.121	17.4 (10.5–24.5)	0.213

* See Table I.
** Mean with 95% confidence limits, μgram equivalents.
***Index of precision. See text.

total darkness underwent gonadal regression. Unfortunately we are unable to perform comparable experiments with *Zonotrichia leucophrys gambelii* since it seems impossible for these birds to feed and drink adequately in continuous *complete* darkness. However, it should be noted that our experiments with *Z. l. gambelii,* involving the shift from long days to short, have given results (gonadal regression) that are apparently similar to those of Wolfson on *J. hyemalis.* The very interesting problem of the synthesis and output of pituitary gonadotropin in total darkness by a bird with a long-day circadian periodicity appears, at present, unapproachable with *Z. l. gambelii.*

Our experiments show that the effect of a long daily photoperiod carries on into the ensuing short days. Therefore, at least in its simplest form, our working hypothesis that each long day results in a fixed logarithmic increment of growth is clearly untenable. However, the apparently linear relationship between growth rate (in cycles $^{-1}$) and the number of days per cycle (Fig. 1), together with the results of Experiment IV, lead to a relatively simple, revised hypothesis. This hypothesis assumes that the gonads are able to derive more growth from the quantum of gonadotropin released by one long day when the long day is followed by one or more short days than when it is followed by another long day because of the longer period for the "use" of the quantum of gonadotropin. However, we do not know definitely whether the quantum of gonadotropin released by a long day is constant or whether it may change as some function of the number of preceding short days. The gonadotropin assays do not supply an answer although the greater accumulation of pituitary gonadotropin in the birds subjected to various L S cycles (Fig. 2; Tables III and IV) and the positive correlation between the gonadotropin concentration in the anterior pituitary and the rate (in cycles $^{-1}$) of gonadal growth (compare Experiments I and II; Fig. 2, Table III) do suggest that the rate of release of gonadotropin is, to some extent, a function of the level of storage of the hormone. The revised hypothesis is illustrated diagrammatically in Figure 4. Under a treatment of daily long photoperiods (Fig. 4a), it is reason-

TABLE IV

The effect of alternation of long days and short days on the concentration of gonadotropin in the anterior pituitary gland of female Zonotrichia leucophrys gambelii Experiment I

Group / Photoperiodic cycle*	Gonadotropin Content per gland** μg. equivalents	λ***
L_1	3.5 (1.6– 7.4)	0.195
L_2	9.9 (7.5–15.9)	0.134
L-S	8.9 (7.6–12.1)	0.121
L-2S	14.6 (11.4–19.2)	0.133
L-3S	14.8 (11.4–18.9)	0.148
L-5S	11.4 (8.7–14.5)	0.132

* See Table I.
** Mean with 95% confidence limits, μgram equivalents.
*** Index of precision. See text.

able to assume that gonadal growth is maximal, for the specific duration of the daily photoperiod, and relatively constant logarithmically for about 30 days (Farner and Wilson, 1957; Farner *et al.*, 1966). This is supported by the linear relationship between the logarithm of gonadal weight and time for 25–30 days after the beginning of photoperiodic stimulation, and also by the fact that gonadal growth is normally limited by the rate of secretion of gonadotropin and not by the inherent growth potential of the gonad (Follett, Farner, King and Morton, unpublished). On the other hand, the logarithmic growth increment in an L 3S cycle probably varies greatly from day to day (Fig. 4b). Since release of gonadotropin is presumably induced only by the long day, the gonadal growth rate would reach a maximum at this time or shortly thereafter. However, the gonadotropin has a persistent effect on gonadal growth mechanisms (as indicated by all bioassay techniques) and thus, whereas the rate of gonadal growth decreases through the three short days, growth does not cease immediately after cessation of gonadotropin release. Figure 4 suggests an explanation of the greater gonadal growth rate per cycle for L 3S as compared to L. The area under the curve represents the amount of gonadal growth (growth rate × time); in cycle L 3S this area is greater than in cycle L. Under natural conditions this would not be expressed because of the daily release of gonadotropin. It can become apparent only when non-stimulatory days are used to extend the duration of action of a single daily "quantum" of gonadotropin. In its present semi-quantitative form the revised hypothesis does not describe the mechanism of the protracted effect of the long photoperiod. However, it is significant that the half-life of gonadotropins in plasma (*e.g.* Catchpole, 1964) is relatively short compared with the duration of their effect on the target organs. It is clear that several alternate hypotheses could be proposed to explain the increase in k (in cycles $^{-1}$). Among these is the possibility of a lag in conversion from a long-day circadian periodicity, of the type that Wolfson (1966) has reported to persist on changing to continuous darkness, to a short-day type periodicity. However, the alternates considered by us, in each case, have proven to be more complex than the hypothesis proposed here.

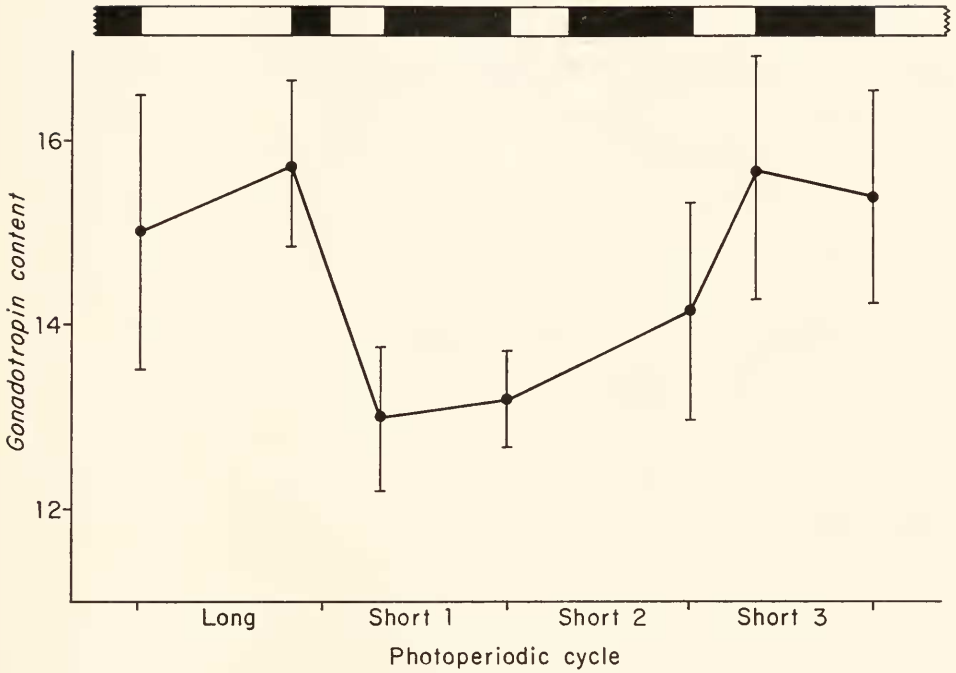

FIGURE 3. Gonadotropin content of the anterior pituitary of males (*Zonotrichia leucophrys gambelii*) in μg. equivalents of NIH-LH in a cycle consisting of one long day (20L 4D) followed by three short days (8L 16D). Black and white bars depict dark and light periods, respectively. Vertical bars define the 95% confidence limits.

In Experiment I there was a close linear relationship between the concentration of pituitary gonadotropin and the number of short days per cycle (Fig. 2). This suggests that synthesis occurs during the short days without release, or at least with a lower rate of release, with a consequent accumulation of gonadotropin proportional to the number of short days. This conclusion is also supported by the ratios of gonadotropin content to the number of days per cycle; these ratios are L, 2.7; L S, 3.3; L 2S, 3.4 and L 5S, 2.6. Particular significance here lies in an apparent separation of the mechanisms that control synthesis and release of adenohypophysial gonadotropin. The absence of a similar relationship in Experiment II is difficult to explain; however, it may also reflect a separation of the mechanisms of control of synthesis and release since we (Follett and Farner, 1966) have shown that the photoperiodic history of an individual bird profoundly affects the storage level of pituitary gonadotropins, a prolonged exposure to short daily photoperiods resulting in a steady increase in concentration (Fig. 2). Thus in Experiment II it is possible that the pituitary gonadotropins were already at maximal level and that further storage was not possible. It is significant in this context that the rates of gonadal growth are essentially similar in Experiments I and II (Table I and Fig. 1), suggesting that the differences in pituitary gonadotropic potency between the groups probably are associated with the control of synthesis rather than with the rate of release.

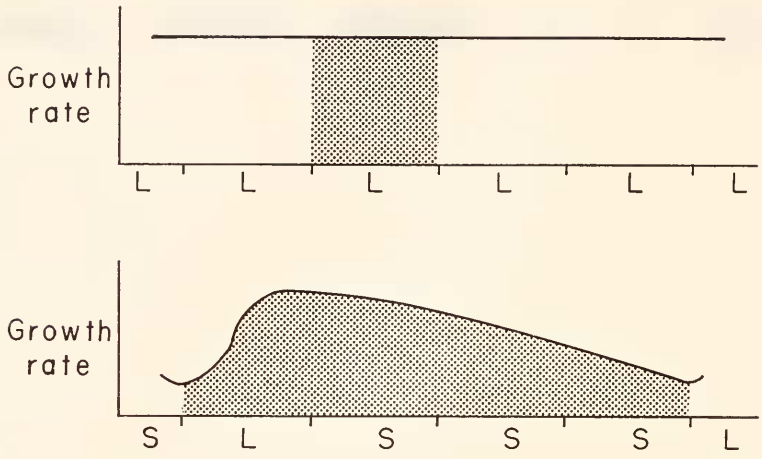

FIGURE 4. Hypothetical gonadal growth rates for *Zonotrichia leucophrys gambelii* under (a) continuous long days (upper) and (b) during a cycle consisting of a long day followed by three short days (lower). The shaded area above is characteristic for each L, *i.e.*, daily. The shaded area below is characteristic of each L 3S cycle.

Experiment III (Fig. 3) was designed to explore more precisely the periods of synthesis and release in an L S cycle and thus assist in the interpretation of Experiments I and II. Although it might be expected that the main release of gonadotropin would occur during the long daily photoperiod no differences were detected in gonadotropins over this time. The simplest explanation must be that rate of synthesis during the long day is equal to the rate of release of hormone with no change in glandular content. During the period of 12 hours following the long daily photoperiod there was a significant drop in pituitary gonadotropins ($P < 0.05$); the rate of synthesis at this time can then be assumed to have decreased from the rate during the long photoperiod whereas there must have been continued release. In any case the decrease supports the case of a short-term "carry-over effect" (see Farner and Follett, 1966) of hypothalamic or pituitary origin that causes continual release of hormone into the dark period. Alternatively one could consider that the main release of gonadotropin does not occur during the long daily photoperiod but subsequent to it; this hypothesis seems unlikely since the maximal rate of testicular growth occurs in continuous light (Farner and Wilson, 1957).

During the final two and one-half days of short photoperiods of the cycle there is an increase in adenohypophysial gonadotropin. Again there appears to be at least a partial separation of the controls of the rates of synthesis and release, the former exceeding the latter. These data provide an experimental basis for rationalization of the results of Experiment I in which the concentration of pituitary gonadotropin is directly related to the number of short days per cycle (Fig. 2).

Finally, it seems probable that the increased rate of gonadal growth (in cycles $^{-1}$) in the groups subjected to L S cycles involves a persistent anabolic action of gonadotropin on the gonad, an action that apparently persists for 7–11 days after the long photoperiod. The increase in pituitary gonadotropins as a function of the

number of short days per cycle in Experiment I provides a further suggestion of separate control of the synthesis and secretion. Although the exact timing of the release of hormone caused by a stimulatory photoperiod remains to be elucidated, it becomes evident after the end of the long daily photoperiod.

Summary

The characteristics of the gonadal photoperiodic responses in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii,* have been examined by the use of cyclic photoperiodic regimes consisting of a day with a long photoperiod followed by *n* days with short, non-stimulatory daily photoperiod, *n* with the range 0–5; responses measured were the rates of gonadal growth and the concentration of pituitary gonadotropin. The gonadotropic effect of a single 20-hour photoperiod extends through at least seven days with short (8-hour) non-stimulatory photoperiods. The apparently simplest interpretation of the results of the experiments suggests that there must be separate, although perhaps not completely independent, control schemes for synthesis and release of pituitary gonadotropin.

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